

FIRST TERTIARY MOLOSSID
(MICROCHIROPTERA : MOLOSSIDAE)
FROM AUSTRALIA: ITS PHYLOGENETIC AND
BIOGEOGRAPHIC IMPLICATIONS

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Petramops creaseri n.gen., n.sp. is described from Middle Miocene freshwater limestones on Riversleigh Station in northwestern Queensland. One of 25 new bat species identified among fossil remains recovered from the Riversleigh deposits, it is Australia's first Tertiary molossid. Its affinities appear to lie outside the modern Australian molossid radiation. It seems likely that bats of the *Petramops* lineage were proficient long-distance fliers which colonized Australia before the Miocene. Subsequent or coincident colonizations of Australia by molossids would have involved species of *Nyctinomus*, *Chaerephon* and *Mormopterus*.

□ Chiroptera, Molossidae, Riversleigh, Miocene, *Petramops creaseri*, biogeography.

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Fossil material referable to a new genus and species of molossid has recently been recovered from Tertiary freshwater limestones on Riversleigh Station, northwestern Queensland (Fig. 1). The Riversleigh fossil deposits cover an area of at least 40 sq. km and appear to comprise a sequence of sediments ranging in age from approximately 25 to 4 My ago (Archer *et al.*, 1986; Archer *et al.*, 1989).

From the remarkably mammal-rich Riversleigh Tertiary deposits, some 25 new species of fossil bats have been identified. These include *Hipposideros* (*Brachhipposideros*) *nooraleebus* Sigé, Hand and Archer (Sigé *et al.*, 1982), *Macroderma godthelpi* Hand (Hand, 1985), *M.* sp. and a number of other hipposiderids, megadermatids, rhinolophids, emballonurids and vespertilionids, as yet undescribed (Hand, 1987).

The bat described here is Australia's first Tertiary molossid, the first representative of bats outside the superfamily Rhinolophoidea to be described from the Riversleigh sediments. The pancontinental family Molossidae is otherwise represented in Australia by five living species whose taxonomy is currently confused (e.g. Hill, 1961; Felten, 1964; Allison, 1978, 1983; Freeman, 1981; Honacki *et al.*, 1982; Legendre, 1984b; Mahoney & Walton, 1988).

In this study, dental morphology is used in an attempt to interpret the phylogenetic position of the Riversleigh fossil with respect to other Australian and non-Australian molossids. A biogeographic hypothesis involving the new molossid is proposed.

Specimens or casts examined in this study include representatives of all species of Australian molossids and subgeneric-level taxa of living non-Australian species. Also examined were specimens or casts of the fossil species: *Mormopterus* (*Hydromops*) *helveticus*, *M.* (*H.*) *stehlini*, *Nyctinomus* (*Nyctinomus*) *engesseri* (see below for discussion of the name *Nyctinomus*), *N.* (*N.*) *leptognathus* and '*Meganycteris monslapidensis*' (Table 2). Fossil specimens not examined but well-enough described or illustrated in the literature to be included in this study were *Cuvierimops parisiensis* (Legendre & Sigé, 1984) and *Mormopterus* (*Neomops*) *faustoi* (Legendre, 1984a, 1985). Other fossil molossids, too poorly represented to include in the phylogenetic analysis, are discussed more briefly.

Repositories of specimens are indicated by prefixes as follows: AM, Australian Museum; SAM, South Australian Museum; BMNH, British Museum (Natural History); AMNH, American Museum of Natural History; QM, Queensland

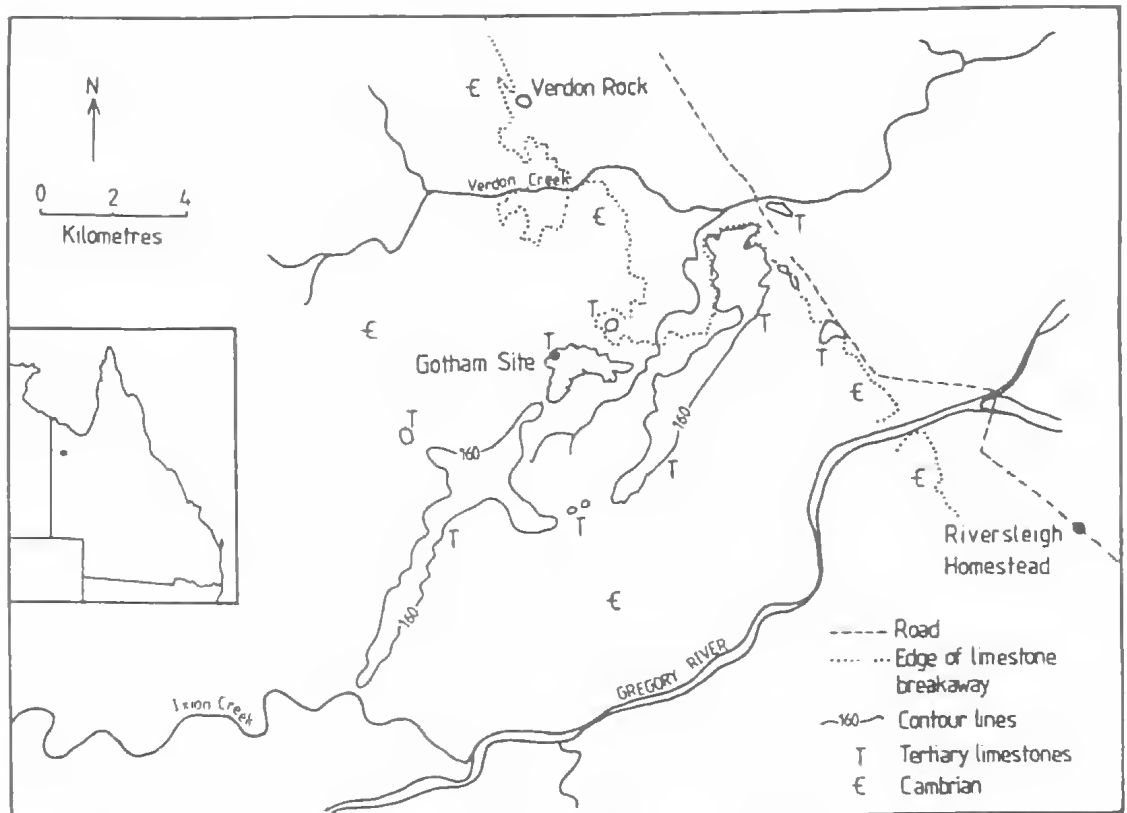


FIG. 1. Map of Riversleigh area showing location of Gotham City Site (after a map prepared by K. Gri mes and modified by H. Godthelp and M. Archer).

Museum; CG, Museum National d'Histoire Naturelle, Paris; SG, Museum d'Histoire Naturelle, Basle; 1970 XVIII, Bayerische Staatssammlung für Paläontologie und historische Geologie, München.

Dental terminology follows Legendre (1985) or is modified as in Fig. 2. Phylogenetic systematic terms used in this paper are summarized in Wiley (1981).

SYSTEMATICS

Order CHIROPTERA Blumenbach, 1779
Suborder MICROCHIROPTERA Dobson, 1875
Superfamily VESPERTILIONOIDEA Gray, 1821
Family MOLOSSIDAE Gill, 1872

Petramops creaseri n.gen, n.sp.

TYPE SPECIES

Petramops creaseri sp. nov.

ETYMOLOGY

The generic name is from the Greek *petra* (rock) and *mops* (bats), and refers to the fossil nature of this new Australian molossid; the gender is masculine.

DIAGNOSIS

This molossid genus differs from all others in the following combination of features: loss of I_3 ; lower molar morphology nyctalodont (as defined by Menu & Sigé, 1971; see DESCRIPTION below); P_4 with rudimentary but distinct metaconid; M^1 with distinct and well developed paraloph and metaloph; M^1 with tall conical hypocone isolated from the protocone and postprotocrista by an obliquely oriented depression; M^3 only moderately reduced, such that the premetacrista is longer than the pre- and postparacristae; lower premolars oriented longitudinally (or only slightly obliquely) in the tooth row; lower molar trigonids with marked anteroposterior compression; M_1 with

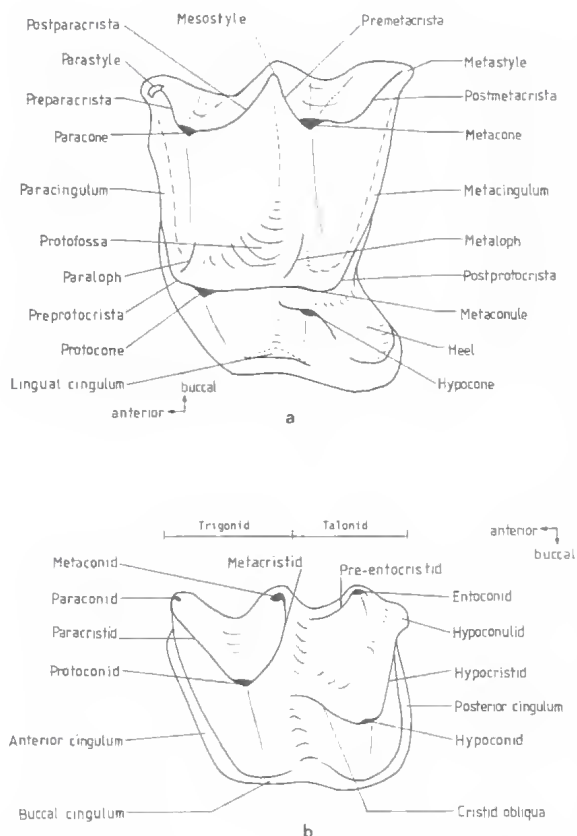


FIG. 2. Tooth terminology for molossids: A, upper tooth; and, B, lower tooth. (After Legendre, 1983; fig. 1).

well-developed paraconid; C_1 much taller than P_4 ; dentary depth tapering posteriorly.

***Petramops creaseri* n.sp.**
Figs 3-4

MATERIAL EXAMINED

HOLOTYPE: QMF 13080, a left dentary containing C_1 , P_4 , M_1 , M_2 , M_3 and alveoli for P_2 .

PARATYPES: QMF 13081, a right M^1 , and QMF 13082, a left M^3 .

ETYMOLOGY

The species is named for Mr Phil Creaser of the National Estate and World Heritage Section of the Department of the Arts, Sport, the Environment, Tourism and Territories. His untiring efforts to find support for the Riversleigh fossil bat research and his indispensable help in collecting fossil-rich limestone on Riversleigh Station are gratefully acknowledged.

DIAGNOSIS

The species diagnosis is the same as that for the genus until additional species are known.

TYPE LOCALITY, AGE, LITHOLOGY AND TAPHONOMY The type locality, Gotham City Site, occurs within the Tertiary sequence of limestone sediments on Riversleigh Station, northwestern Queensland (Fig. 1). It occurs in Ray's Amphitheatre at a level interpreted to be stratigraphically above the Gag Site (Hand, 1985) and Ringtail Site but below Henk's Hollow Site (Flannery & Archer, 1987) and Jaw Junction Site (Archer *et al.*, 1989).

On the basis of its mammal fauna (at least 24 species of marsupials and bats), the Gotham City deposit is interpreted to be of Middle Miocene age and to be younger than the Riversleigh Dwornamor and Upper Site Local Faunas and the South Australian Ditjimanka and Kutjamarpu Local Faunas (Woodburne *et al.*, 1985; Archer *et al.*, 1989) but older than the Riversleigh Henk's Hollow Local Fauna. The detailed stratigraphy of the Riversleigh sites and their relationships to those of South Australia are now under study.

The sediment is fine-grained, argillaceous freshwater limestone. Taphonomically, the Gotham fossil material is thought to represent the remains of prey collected by the megadermatid, *Macroderma* sp. The remains are consistent in size and fragmentation with prey remains recovered from roosts of the Australian megadermatid, *Macroderma gigas*, the latter's closest living relative.

DESCRIPTION

The dentary is represented by the holotype QMF 13080 (Fig. 3). It decreases markedly in depth from C_1 to below the posterior root of M_3 . The large mental foramen occurs below the alveoli for P_2 , the steep symphysis extending posteriorly to this same point. The mandibular foramen is not preserved. Two small foramina occur immediately adjacent to the symphysis midway between the alveolar border and the base of the dentary. The larger dorsal foramen is closer to the symphysis than the smaller, more ventral foramen. The posterior margin of the ascending ramus inclines at an angle of about 30° to the horizontal.

The lower dental formula is $1_{1,2} C_1 P_{2,4} M_{1,2,3}$. The incisors are unknown.

The C_1 is surrounded by a basal cingulum on which are developed minute swellings at the antero-lingual high point and postero-buccal low point of the cingulum. Postero-lingually, a very

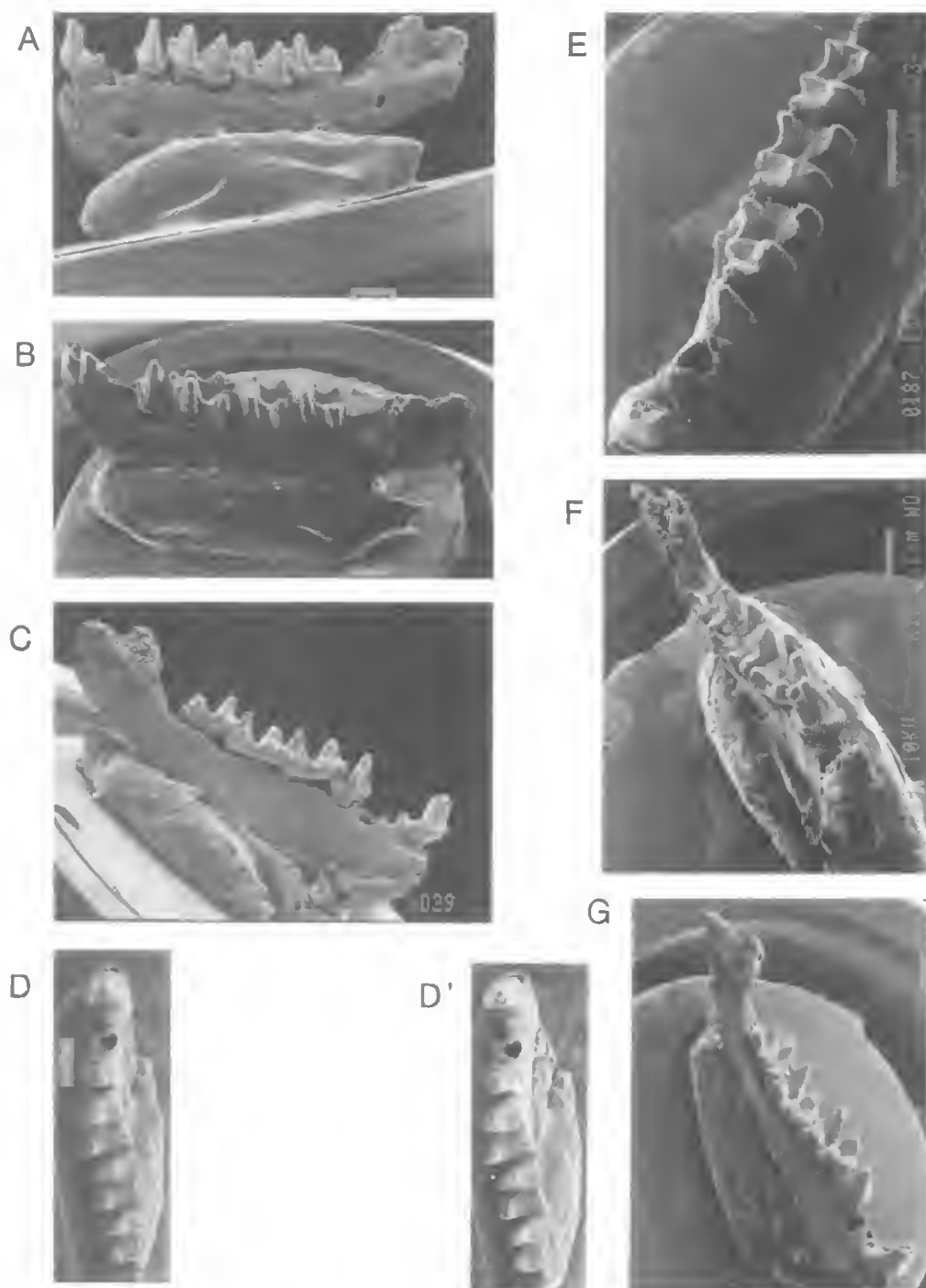


FIG. 3. *Petramops creaseri* from the Gotham City Local Fauna, Riversleigh Station, northwestern Queensland. QMF 13080, holotype, left dentary containing C₁, P₄, M₁, M₂, M₃ and alveoli for I₁, I₂ and P₂. A, buccal view; B, oblique buccal view; C, lingual view; D-D', stereopairs occlusal view; E, antero-occlusal view showing alveoli for P₂; F, anterior view showing alveoli for I_{1,2}; G, oblique-lingual view. Scale indicates 1 mm.

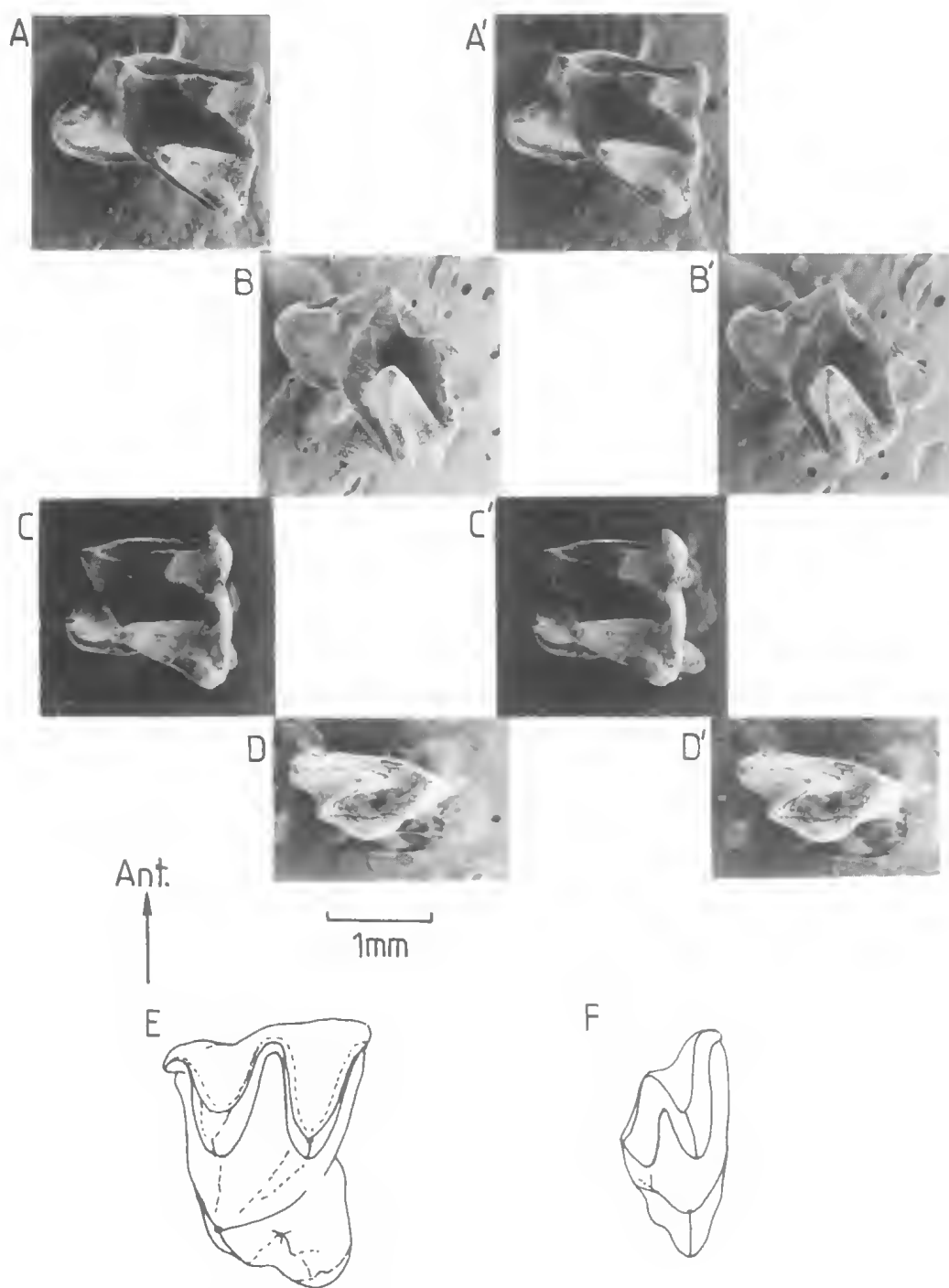


FIG. 4. *Petramops creaseri*. Paratypes. QMF 13081, a right M^1 : A-A', stereopairs, oblique-occlusal view; B-B¹, stereopairs, oblique view; C-C', stereopairs, occlusal view. QMF 13082, a left M^2 : D-D', stereopairs, oblique-occlusal view. Camera-lucida drawings (X 16) in oblique-occlusal view of, E, paratype QMF 13081 and, F, paratype QMF 13082 for comparison with camera-lucida drawings of molossid teeth in Fig. 5.

large cingular cusp contributes to the formation of a pronounced posterior heel, making the lingual face of the tooth markedly longer than the buccal face. This postero-lingual cusp is separated from the protoconid by a wide, shallow facet that passes transversely across the tooth. The lingual cingulum is much higher but narrower and less distinct than the buccal basal cingulum and at one point merges with the swollen postero-lingual edge of the protoconid. The posterior face of the protoconid is wide and conspicuously flattened, being semicircular in horizontal section. On the antero-lingual face, rising from the cingular swelling, a poorly-defined vertical crest is developed. The root of the tooth is very well-developed and posteriorly curved. The tip of the crown is missing.

The P₂ is represented only by alveoli in the holotype. The two alveoli are oblique in the tooth row, the smaller and anterior one being more buccally situated. The P₂ appears to have been a double-rooted and well developed tooth approximately the same length as P₄.

The P₄ has two roots, the posterior being longer and wider than the anterior root. There is one very large median cusp (the protoconid), a well-developed rudimentary metaconid that is approximately two-thirds the crown height of the protoconid, a tiny antero-lingual cingular cusp and a smaller postero-lingual cingular cusp. The nearly vertical anterior face of the tooth is anteriorly convex and bears a vertical crest connecting the protoconid to the antero-lingual cuspule. The protoconid is connected to the metaconid by a short transverse crest. The posterior face of the crown is flattened in a similar fashion to C₁, as is the lingual face of the metaconid. Where these two flattened faces meet, a vertical crest is formed which extends from the tip of the metaconid to the postero-lingual cingular edge of the crown. The almost angular postero-lingual corner of the crown is markedly extended such that the lingual length of the tooth is much greater than the buccal length and the posterior portion of the crown is wider than the anterior portion. The postero-lingual corner of the P₄ cradles the paraconid of M₁. The basal cingulum of the crown is much narrower and less distinct on the lingual side than on the buccal, anterior or posterior sides. In horizontal section, the crown is roughly triangular in shape with the antero-buccal face being slightly convex, the postero-buccal face flattened and the antero-lingual face gently concave. In its height the P₄ protoconid exceeds all crowns except C₁.

The M₁ has two roots and six distinct cusps, the hypoconulid being a small cingular cusp. In height the protoconid exceeds the hypoconid, which exceeds the subequal paraconid, metaconid and entoconid. The trigonid is much narrower than the talonid, in which a deep fossa is developed anteriorly. All cusps are interconnected by crests. The paracristid and metacristid are subequal in length, their paraconid, protoconid and metaconid contributions being approximately equal. The cristid obliqua is uncurved in occlusal view and contacts the trigonid just buccal to the point directly below the junction of components of the metacristid. There is an inflexion along the cristid obliqua at a point closer to the hypoconid than the trigonid. The hypocristid extends from the hypoconid directly to the hypoconulid, thus isolating the entoconid and exhibiting the nyctalodont pattern defined by Menu and Sigé (1971). An inflexion in the hypocristid also occurs closer to the hypoconid than the hypoconulid, reflecting the almost vertical rise from the talonid basin of the hypoconid before lingually recurving. The protoconid, while crescent-shaped like the hypoconid, is more lingually directed.

A steeply declining crest (pre-entocristid) links the entoconid to the trigonid at the base of the M₁ metaconid. The paracristid is orientated antero-lingually. The metacristid is close to being transverse if not also antero-lingually orientated to the long axis of the molar row, reflecting the marked compression of the trigonid. The cristid obliqua is more antero-lingually directed than the paracristid. The hypocristid parallels the metacristid. The pre-entocristid is lingually concave. There is a well-developed continuous anterior, buccal and posterior cingulum terminated near its antero-posterior end for contact with the flattened posterior face of P₄ and near its postero-lingual end by a notch for the anterior cingulum of M₂. A low cingular swelling may be discerned lingual to the trigonid basin between the bases of the metaconid and paraconid. Nevertheless, the trigonid basin is open lingually, as is the talonid at a point near the base of the trigonid.

The M₂ is described here only in so far as it differs from M₁. The M₂ is shorter than M₁, with the trigonid almost as wide as the talonid. The paracristid and metacristid are more transversely oriented with respect to the tooth row, the paraconid and metaconid more closely approaching each other on the more antero-posteriorly compressed trigonid. The cristid obliqua is slightly curved in occlusal view, this

inflexion occurring approximately three-quarters of the distance from the hypoconid to the trigonid.

The M_3 is described only in so far as it differs from M_1 . The M_3 is much shorter than M_1 and M_2 . The trigonid is noticeably more antero-posteriorly compressed. The trigonid is subequal in width (if not wider) than the talonid. The paracristid is longer than the metacristid, its paraconid contribution being greater than the metaconid contribution to the metacristid. The point of inflexion in occlusal view in the cristid obliqua occurs very close to the metaconid.

Meristic gradients along the lower tooth row are as follows. The protoconids of M_1 and M_2 appear to be subequal in height and much higher than that cusp on M_3 . The entoconids also show this pattern. The paraconids of M_1 to M_3 are subequal in height, as are the metaconids. The hypoconids appear to decline in height from M_1 to M_3 . The hypoconulid of M_3 appears to be less well-developed than that of M_1 and M_2 . The paracristids, metacristids and hypocristids decrease slightly in length posteriorly. The pre-entocristids of M_1 and M_2 are subequal in length, as are the cristids obliqua. These crests are markedly shorter in M_3 . The angles formed between the protoconid and paraconid contributions to the paracristid of $M_{1,2}$ and the protoconid and metaconid contributions of the metacristid become more obtuse posteriorly. The angle formed between the paracristids and metacristids of $M_{1,2}$ become more acute posteriorly.

The upper dentition is known only from the paratypes, a right M^1 and left M^3 .

The M^1 (QMF 13081) has three roots and six principal cusps. The metacone is taller than the broken paracone, which probably would have been slightly taller than the protocone. The protocone is taller than the very pronounced hypocone; this, in turn, is taller than the metastyle, which is taller than the parastyle. The paracone and metacone are sharply crescentic, being deeply excavated buccally. A well-developed paraloph extends lingually from the base of the paracone to the tip of the protocone. A well-developed metaloph extends antero-lingually from a point just antero-buccal of the base of the metacone to a point approximately halfway towards the protocone tip. A deep, confined protofossa is defined by the paraloph, metaloph and adjacent bases of the paracone, metacone and protocone. The pre- and postmetacristae are subequal in length and much longer than the postparacrista, which is longer than the preparacrista. The preparacrista meets the well-developed, anteriorly-oriented parastyle at a

right angle. The antero-buccal flank of the massive parastyle is smoothly rounded as is the buccal side of the mesostyle and the postero-buccal flank of the metastyle. The postparacrista and premetacrista contact at the mesostyle which, however, is not cuspidate. A mesostylar shelf extends from the well-developed parastyle to the distinct but non-inflexed metastyle. The angle formed between the pre- and postparacristae is approximately 55° , which is slightly greater than the comparable angle formed between the pre- and postmetacrista (approximately 45°).

Anteriorly the M^1 preprotocrista forms a broad shelf (the paracingulum) which reaches the parastyle. The postprotocrista becomes continuous with the posterior cingulum (forming the metacingulum) at a point posterior to the base of the metacone. From this point, the paracingulum continues buccally to meet the metastyle while the posterior cingulum swings slightly postero-lingually, then lingually and then anteriorly to meet the lingual cingulum at a point of pronounced cingular swelling (i.e. at the most postero-lingual point of the tooth). Together the posterior and lingual cingula enclose the well-defined, lingually-directed heel. The antero-lingual basal cingulum terminates at the posterior protocone base.

The heel of M^1 is dominated by the tall conical hypocone which is isolated from the protocone and the postprotocrista by a shallow obliquely oriented depression or valley. Approximately at a right angle to this depression a postero-lingually oriented vertical crest links the antero-buccal base of the hypocone to the hypocone tip and the most postero-lingual point of the tooth (i.e. the swollen postero-lingual portion of the basal cingulum). The heel extends anteriorly to a point level with, but basal to, the mesostyle and postero-buccally to the junction of posterior cingulum and postprotocrista. The heel is widest around the postero-lingual base of the crown and longest (antero-posteriorly) at the level of the protocone. In occlusal view, the heel is sharply-defined lingually by a conspicuous notch (or change in direction of slope) in the basal lingual cingulum. The tooth has three roots, subequal paracone and metacone roots and a larger protocone root.

The M^3 (QMF 13082) is described in so far as it differs from M^1 . The metacone (which is damaged) appears to have been shorter than the paracone and subequal in height to the very poorly defined (and worn) parastyle which meets the preparacrista at a very obtuse angle. A notch for the M^2 metastyle is developed in the anterior cingulum near the

TABLE 1. Measurements (following Sigé *et al.*, 1982) of the holotype QM F13080 and paratypes QM F13081 and QM F13082 of *Petramops creaseri* from the Gotham City Local Fauna, Riversleigh Station.

CHARACTER	HOLOTYPE QM F13080	PARATYPES	
		QM F13081	QM F13082
C ₁ — M ₁	6.80		
P ₄ — M ₁	4.83		
M ₁ — M ₂	4.13		
C ₁ length	1.19		
C ₁ width	1.09		
P ₄ length	0.94		
P ₄ width	0.90		
M ₁ length (<i>in situ</i>)	1.48		
M ₂ length (<i>in situ</i>)	1.44		
M ₁ length (<i>in situ</i>)	1.40		
M ₁ trigonid length	0.72		
M ₁ talonid length	0.83		
M ₂ trigonid length	0.65		
M ₂ talonid length	0.71		
M ₁ trigonid length	0.48		
M ₁ talonid length	0.78		
M ₁ trigonid width	1.00		
M ₁ talonid width	1.24		
M ₂ trigonid width	1.02		
M ₂ talonid width	1.22		
M ₁ trigonid width	0.89		
M ₁ talonid width	0.85		
M ¹ length		1.54	
M ¹ width		1.69	
M ² length			0.85
M ² width			1.62

antero-buccally oriented parastyle. There is no heel or postero-lingual development of the crown beyond the protocone. There is no postmetacrista or metastyle. The premetacrista, however, appears to remain longer than the pre- and postparacristae, and the postmetacrista may be represented by a noticeable swelling on the postero-buccal flank of the metacone.

Measurements of holotype and paratypes are given in Table 1. Measurements were made to the nearest 0.01mm using a Wild MMS 235 Digital Length-Measuring Set attached to a Wild M5A Stereomicroscope.

COMPARISONS

Petramops creaseri clearly belongs to the family Molossidae, which is distinguished by the following

combination of dental and cranial features (Dobson, 1878; Miller, 1907; Hill, 1961):

1. skull low and flattened, with braincase not greatly inflated;
2. skull lacks postorbital processes;
3. posterior orifice of antorbital canal not enlarged;
4. premaxillaries with nasal branches present or absent; when present forming two palatal foramina, when absent allowing the formation of one which extends to or beyond the roots of the incisors;
5. single pair of large upper incisors occupying the centre of the space between the canines;
6. P² reduced or absent;
7. P⁴ with well-developed anterior cingular cusp;
8. traces at least of a hypocone on M¹ and (variably) on M²;
9. development on M¹⁻³ of a paracingulum which is continuous with the preprotocrista;
10. two lower sub-caniniform premolars;
11. P₄ with postero-lingual extension that cradles paraconid of M¹.

Of these features, the last four are present in the material referred to *Petramops creaseri*.

The family comprises approximately 80 living species (Honacki *et al.*, 1982) and more than 15 fossil species (Legendre, 1985; Table 2). Living species have recently been referred to as many as 12 genera (e.g. Freeman, 1981; Honacki *et al.*, 1982) or as few as nine (e.g. Legendre, 1984b). Fossil species are referred to an additional two genera (Legendre, 1984a; 1985). Representative specimens of generic and subgeneric groups recognized in these recent studies have been examined and compared with the new Australian fossil species.

The most recent systematic revision of the family Molossidae is that of Legendre (1984b). From analysis of dental characters in living and fossil Molossidae, Legendre (1984b, 1985) recognized three subfamilies: the Tadaridinae, Molossinae and Cheiromelinae. In his revision Legendre erected the new genus *Rhizomops* in which he placed the living American tadaridine *Tadarida brasiliensis* and a number of Tertiary and Pleistocene taxa from the Old and New Worlds. Species of *Rhizomops* were considered to be more plesiomorphic than any other living tadaridines, lacking several derived features found in other species of *Tadarida*. Legendre retained *Tadarida* for all other species usually referred to that genus (e.g. by Freeman, 1981; and by Honacki *et al.*, 1982). In *Tadarida* he also included *Chaerephon* and *Mops* as subgenera. The basic taxonomic framework proposed by Legendre, including

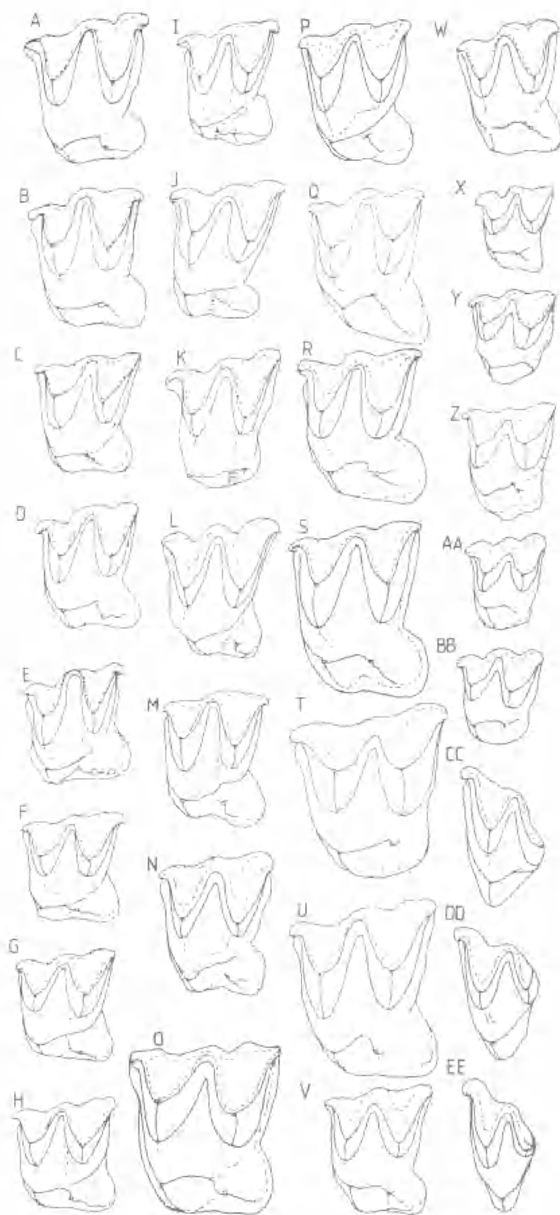


FIG. 5. Camera-lucida drawings (X 8) of M^1 in representative molossids discussed in text: A, AM M8509 *Mormopterus* (*Micronomus*) *beccarii*; B, AM M8904 *M. (M.) planiceps*; C, AM M5188 *M. (M.) loriae*; D, SAM M8372 *M. (M.) loriae*; E, AM M5041 *M. (M.) ? norfolkensis*; F, CG 1983-2257 *Mormopterus* (*Mormopterus*) sp. (?South American); G, CG 1983-2268 *M. (M.) minutus*; H, CG 1983-2269 *M. (M.) minutus*; I, AMNH 165626 *M. (M.) kalinowski*; J, BMNH 66.6060 *M. (M.) jugularis*; K, AMNH 217024 *M. (Platymops)* *setiger*; L, BMNH 73.522 *M. (Sauromys)* *petrophilus*; M, AM M8132 *Rhizomops brasiliensis*; N, AMNH 245636 *Nyctinomus aegyptiacus*; O, AM M7190 *Nyctinomus australis*; P, AMNH 78219 *Nyctinomops laticaudata*; Q, AM M9951 *Chaerephon pumila*; R, AM M9178 *C. plicata*; S, AM M135 *C. jobensis*; T, AMNH 88115 *Otomops martiniensis*; U, AMNH 161862 *Mops condylura*; V, AMNH 241087 *Mops (Xiphonycteris)* *spurrelli*; W, AMNH 181533 *Molossops temminckii* (X 4); X, AMNH 94625 *M. (Cynomops)* *brachymeles* (X 4); Y, AMNH 48855 *Myopterus albatrus* (X 4); Z, AMNH 97022 *Eumops perotis* (X 4); AA, AMNH 178692 *Promops centralis* (X 4); BB, AMNH 123306, *Molossus ater* (X 4). Camera-lucida drawings (X 8) of the M^1 of representative molossids discussed in text: CC, BMNH 66.6060 *Mormopterus (M.) jugularis*; DD, AM M9951 *Chaerephon pumila*; EE, BMNH 73.522 *M. (Sauromys) petrophilus*.

Following the provision of Article 40a of the International Code of Zoological Nomenclature (1985), the subfamily Tadaridinae Legendre, 1984b is retained despite the generic seniority of *Nyctinomus* over *Tadarida*.

COMPARISON WITH LIVING FORMS

The Riversleigh fossil molossid differs from species of *Molossus*, *Molossops*, *Eumops*, *Promops*, *Myopterus* and *Cheiromeles* in its tall, conical, isolated hypocone and well-developed heel on M^1 (Fig. 5), its only moderately reduced M^3 and its antero-posteriorly compressed trigonids on M_{1-3} . In these features it is more similar to species of Legendre's (1984b, p.426) subfamily Tadaridinae, which includes all other genera of living molossids.

Among tadaridine species groups, the Riversleigh fossil probably most closely resembles in dental morphology the American species *Rhizomops brasiliensis*. It shares a number of features with *R. brasiliensis* which are not all shared with other species of *Nyctinomus*. These features include nyctalodont lower molars; P_4 with rudimentary metaconid; M^1 with well-defined

recognition of the genus *Rhizomops*, is largely adopted in this paper (but see discussion).

Recently, however, Mahoney and Walton (1988) have noted that the name *Nyctinomus* has priority over *Tadarida* Rafinesque 1914. Evidently *Nyctinomus* was erected by Geoffroy in 1813, and not 1818 as usually reported (see Mahoney & Walton for full discussion). In this paper the name *Nyctinomus* replaces *Tadarida* throughout.

paraloph and metaloph; M^3 with less well-developed paraloph; M^1 hypocone tall and isolated from protocone and postprotocrista by a depression; P_2 and P_4 oriented longitudinally rather than transversely in the axis of the lower tooth row (see Fig. 6), and M^3 only moderately reduced. The Australian fossil differs from the living American species in, among other features, its loss of I_3 , marked antero-posterior compression of M_{1-3} trigonids, and less postero-lingually extended heel on M^1 .

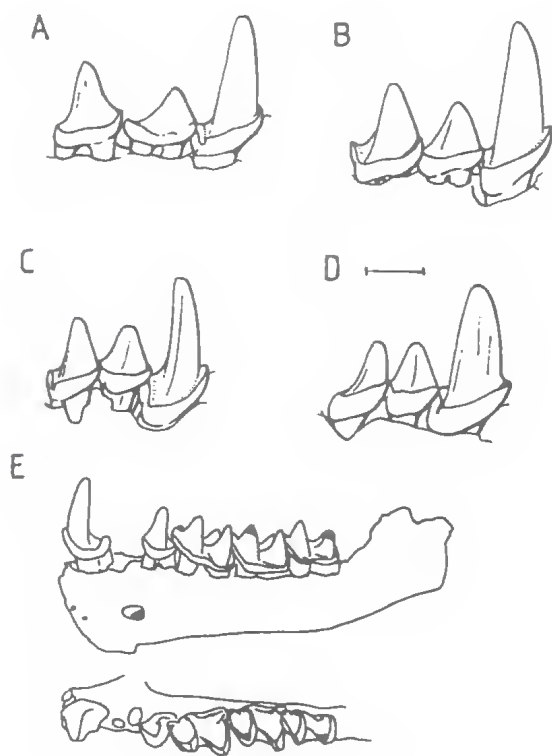


FIG. 6. Orientation of lower premolars (P_2 and P_4) in the tooth row of representative molossids: Type A, premolars longitudinal in the tooth row, e.g., *Nyctinomops macrotis* BMNH 20.7.14.33; Type B, premolars only slightly oblique to the tooth row, e.g. *Nyctinomops teniotis* BMNH 97.11.10.2; Type C, premolars more oblique to the tooth row, e.g., *Chaerephon plicata* BMNH 9.1.5.508; and, Type D, premolars transverse to the tooth row, e.g., *Mops mops* BMNH 60.1597. The Riversleigh molossid (E, buccal and occlusal views) appears to be most similar to Type B. Scale indicates 1 mm. (After Legendre, 1983; fig. 2).

With species of the tadaridine *Nyctinomops* from Central and South America, the Riversleigh fossil shares the loss of I_3 ; nyctalodont lower molars; a well-developed paraloph and metaloph on M^1 ; a poorly-developed paraloph on M^3 ; a tall isolated hypocone on M^1 ; P_2 and P_4 in the longitudinal axis of the lower tooth row, and marked antero-posterior compression of M_{1-3} trigonids. Species of *Nyctinomops* differ from the Australian fossil in the loss of the P_4 metaconid, a more reduced M^3 and convergent paraloph and metaloph on M^1 .

Species of the tadaridine genus *Mormopterus* are commonly divided into three subgeneric groups: species of *Mormopterus*, *Sauromys* and *Platymops* (e.g. Freeman, 1981; Honacki *et al.*, 1982). Legendre (1984b) further divided the genus into the subgenera *M.* (*Mormopterus*) for African, Madagascan and American species of *Mormopterus* (as well as the poorly-known Asian species *M. doriae*), and *M.* (*Micronomus*) for Australasian species.

The monotypic southern African species *M.* (*Sauromys*) *petrophilus* differs from the Australian fossil species in, among other features, its myotodont lower molars (where the hypocristid extends from the hypoconid to the entoconid, isolating the hypoconulid), its loss of the metaloph on M^1 and its more reduced M^3 .

The monotypic East African species *M.* (*Platymops*) *setiger* differs from the Riversleigh molossid in its myotodont lower molars, its loss of the metaconid on P_4 , its lack of both paraloph and metaloph on M^1 , and the transverse orientation of P_2 and P_4 in the lower tooth row. It further differs from the Australian fossil in the connection by crests of the anterior portion of the postprotocrista to the poorly-developed hypocone on M^1 .

African and Madagascan species of *Mormopterus* (e.g. *M. jugularis*) differ from the Riversleigh molossid in retention of I_3 , their myotodont or sub-myotodont lower molars, loss of the metaconid on P_4 , and the connection by crests of the postprotocrista to the hypocone on M^1 .

Central and South American species of *Mormopterus* (e.g. *M. kalinowski*) are more similar to the Riversleigh molossid but differ in their myotodont or sub-myotodont lower molars and the loss of the P_4 metaconid.

The poorly-known *M. doriae* from Sumatra appears to be no longer represented in world museum collections, the type specimen apparently being lost from the Genova Museum during a flood. Judging from descriptions by Anderson (1907), Hill (1961) and Legendre (1984b), this

Asian species appears to differ from the Australian fossil at least in retaining the I_3 . In his comparison of *M. doriae* with other species of *Mormopterus*, Anderson (1907) concluded that it differs only slightly from the Malagasy *M. jugularis* and that it is much more similar to African *Mormopterus* species than Australasian ones.

Australasian (i.e. Australian, New Guinean and Molucca Island) species of *Mormopterus*, (*beccarii*, *planiceps*, *norfolkensis*) differ from the Riversleigh species in their loss of the P_4 metaconid, the connection of the M^1 postprotocrista and hypocone by crests, and the transverse orientation of P_2 and P_4 in the lower tooth row. *Mormopterus beccarii* further differs from the Riversleigh fossil in its myotodont lower molars.

All other living species of tadaridine bats are referred to the *Nyctinomus*, *Chaerephon*, *Mops* and *Otomops* species groups, which are considered to comprise as many as four genera (Freeman, 1981) or as few as two genera (Legendre 1984b, who includes *Chaerephon* and *Mops* as subgenera in *Nyctinomus*).

Species of *Nyctinomus* (*Nyctinomus*) differ from the Riversleigh molossid in the loss of the P_4 metaconid, the lack of the metaloph on M^1 and the lack of marked antero-posterior compression of the lower molar trigonids. The large African forms further differ from the Australian fossil in the connection of the M^1 hypocone to the postprotocrista by crests, lack of a paraloph on M^1 and more reduced M^3 . Most *Nyctinomus* species lack the I_3 , and in this way resemble the Riversleigh fossil, but one species, the Palearctic *N. teniotis*, retains the I_3 .

African, Asian and Australian species of *Chaerephon* differ from the Australian fossil in the lack of the P_4 metaconid, the lack of paraloph and metaloph on M^1 , the presence of crests linking hypocone to postprotocrista, a more reduced M^3 and the lack of antero-posterior compression of the lower molar trigonids.

African, Malagasy and Asian species of *Mops* (including *Xiphonycteris*), differ from the Riversleigh fossil in the same features as do species of *Chaerephon*, but in some African species a weak paraloph is present. Species of *Mops* further differ from the fossil in the transverse orientation of the P_2 and P_4 in the lower tooth row and the distal opening of the protofossa on M^1 .

Afroasiatic species of *Otomops* differ from the Riversleigh fossil in the same features that *Chaerephon* does, but have a less reduced M^3 . Thus, they more closely resemble both the

Riversleigh fossil and non-African species of *Nyctinomus* (*Nyctinomus*).

COMPARISON WITH FOSSIL FORMS

The Miocene species from Riversleigh is one of 13 Tertiary molossids now known. These are referred to five genera: *Nyctinomus*, *Mormopterus*, *Rhizomops*, *Cuvierimops* and *Wallia* (Table 2).

The oldest identified molossid, the North American Late Eocene (Uintian) *Wallia scalopidens* Storer, 1984, is known from four isolated upper molars. It was originally described as a proscalopid insectivore, but was recognized as a molossid by Legendre (1985). Its affinities with other molossids are not clear, but from Storer's (1984) figures and description it appears to resemble the Riversleigh fossil in most of its features, including the separation of the hypocone from the postprotocrista by a shallow valley and its only moderately reduced M^3 . However, it seems to differ in M^1 in its poor heel development, "low" hypocone and indistinct paraloph and metaloph (? para- and metaconule of Storer) and, in M^3 , in its antero-lingually directed parastyle and bulbous protocone. Legendre (1985) has tentatively placed *Wallia scalopidens* in the Tadaridinae, the subfamily to which all Tertiary fossil molossids are currently referred.

Late Eocene and early Oligocene French and Spanish species of the genus *Cuvierimops* appear to be early members of the subfamily Tadaridinae (Legendre, 1985). They are characterised by: nyctalodont lower molars; P_4 with metaconid; a well-defined, conical, isolated hypocone on M^{1-2} separated from the protocone and postprotocrista; paraloph and metaloph on M^1 ; and slightly reduced M^3 (Legendre & Sigé, 1984) — features also shared with the Australian Miocene fossil. However, the type species *C. parisiensis* differs from the Riversleigh form in its remarkably short C_1 (which is only just taller than the P_4) and less well-developed heel and hypocone crests on the upper molars.

The late Oligocene species *Mormopterus* (*Neomops*) *faustoi* (Paulo Couto, 1956) from Brazil is the sole species of the subgenus (erected by Legendre, 1984a) and South America's oldest fossil bat (Paulo Couto & Mezzalana, 1971). It differs from the Riversleigh species in its retention of I_3 , its myotodont lower molars and its lack of paraloph and metaloph on M^1 .

TABLE 2. Tertiary representatives of the family Molossidae (after Hand, 1984).

		EUROPE	AFRICA	ASIA	AUSTRALIA	N.AMERICA	S.AMERICA
PLIOCENE							
MIOCENE	<i>Nyctinomus teniotis</i> ¹³	X					
	?Chiroptera, cf. Molossidae ¹²	X	X				
	<i>Nyctinomus engesseri</i> ¹¹	X					
	<i>Mops monslapidensis</i> ¹⁰	X					
	<i>Nyctinomus leptognathus</i>	X					
	Tadaridinae indet. ⁹	X					
	<i>Petramops creaseri</i> ⁸				X		
OLIGOCENE	<i>Mormopterus (Hydromops) helveticus</i> ⁷	X					
	<i>Mormopterus (Hydromops) stehlini</i> ⁷	X					
	<i>Rhizomops</i> cf. <i>R. brasiliensis</i> ³	X					
	<i>Mormopterus (Neomops) faustoi</i> ⁶						X
EOCENE	Tadaridinae indet. ⁵	X					
	<i>Cuvierimops</i> sp. ³	X					
	<i>Cuvierimops parisiensis</i> ⁴	X					
	<i>Cuvierimops</i> spp. ³	X					
	<i>Wallia scalopidens</i> ²					X	
	Vespertilionoidea ? Molossidae ¹					X	
PALEOCENE							

¹McKenna *et al.*, 1962; Legendre 1985²Storer, 1984; Legendre, 1985³Legendre, 1985⁴Legendre and Sigé, 1984⁵Sigé, 1971; Legendre, 1985⁶Paula Couto, 1956; Paula Couto and Mezzalana, 1971; Legendre, 1984a⁷Revilliod, 1920; Legendre, 1984a⁸Hand and Archer, 1985⁹Adrover, 1968; Legendre, 1985¹⁰Rachl, 1983; Legendre, 1985; Mahoney and Walton, 1988¹¹Lavocat, 1961; Engesser, 1972; Rachl, 1983; Mahoney and Walton, 1988¹²Sigé, 1982¹³Aguilar *et al.*, 1985; Legendre, 1985; Mahoney and Walton, 1988

The first appearance of species of *Rhizomops* in the fossil record occurs in France in Oligocene-Miocene transitional sediments (Legendre, 1985, fig. 16; Table 2). This form, described as *Rhizomops* sp. cf. *R. brasiliensis*, differs from the Riversleigh fossil (and modern *Rhizomops brasiliensis*) in, among other features, the development of the metaloph which arises from the lingual base of the metacone rather than the anterior flank of the metacone (Legendre, 1985).

The French Early Miocene species *Mormopterus (Hydromops) stehlini* and the middle Miocene species *M. (H.) helveticus* from deposits in France, Germany and Switzerland, differ from the Australian Miocene species in: their myotodont lower molars; loss of the P₄ metaconid; lack of the paraloph and metaloph on M¹; presence of crests on M¹ linking the hypocone and postprotocrista; M³ more reduced such that the premetacrasta is

shorter than the postparacrasta; P₂ and P₄ oriented transversely in the lower tooth row, and lack of antero-posterior compression of the lower molar trigonids. Two German Steinberg species, described by Rachl (1983) as *M. kalorhinus* and *M* sp., have been synonymised with *M. (H.) helveticus* by Legendre (1985).

The Middle Miocene species *Nyctinomus engesseri* from deposits in Germany, Switzerland and Morocco, and the slightly older German *N. leptognathus*, differ from the Riversleigh molossid in their retention of I₃ and absence of P₄ metaconid. *Nyctinomus leptognathus* is further distinguished by its lack of the paraloph on M¹ and presence of crests on M¹ linking the hypocone to the postprotocrista.

The Recent species *N. teniotis* first appears in the fossil record in the Late Miocene Salobrena deposit in Spain. It differs from the Australian fossil



FIG. 7. Hypothesis of phylogenetic relationship of the Riversleigh fossil molossid (*Petrarmops creaseri*) to living and fossil molossids based on dental characters. Potential apomorphies include: 1, M^1 with heel and tall isolated hypocone, little reduced P_2 , lower molars with well developed paraconids; 2, very short C_1 , loss of I_3 ; 3, on M^{1-2} hyper-development of hypocone and crests emanating from hypocone; 4, loss of I_3 ; 5, low coronoid process; 6, loss of P_4 metaconid; 7, low coronoid process; 8, upper incisors parallel, on M^{1-2} paraloph and metaloph convergent, M_3 reduced; 9, on M^{1-2} disappearance of metaloph, regression of paraloph and hypocone linked by crests to postprotocrista; 10, M^3 reduced; 11, upper incisors parallel, on M^{1-2} hypocone reduced and protofossa open posteriorly; 12, on M^{1-2} hypocone and heel reduced and paraloph and metaloph absent, P^2 large, P_2 elongated; 13, M^3 reduced; 14, $P_{2,4}$ relatively transverse in jaw; 15, on M^{1-2} hypocone reduced and protofossa more open posteriorly; 16, myotodonty or sub-myotodonty of M_{1-3} ; 17, on M^{1-2} loss of metaloph and protofossa closed; 18, loss or reduction of P^2 ; 19, myotodonty of M_{1-3} ; 20, on M^{1-2} hypocone crests parallel to long axis of tooth row, P^2 lost or reduced to a spicule; 21, on M^{1-2} hypocone reduced and regression of paraloph and metaloph, $P_{2,4}$ elongated, P_2 with second cusp; 22, $P_{2,4}$ transverse in jaw; 23, on M^{1-2} metaloph absent and protofossa tending to open posteriorly, M^3 reduced; 24, upper incisors with internal cingular cusp; 25, P^2 present, nyctalodont and myotodont lower molars, lower incisors with V-shaped indentation; 26, on M^{1-2} hypocone and heel reduced, upper incisors with two cusps. (See text, and also Legendre, 1984a, b, 1985).

species in features described above for living species of *Nyctinomus* (*Nyctinomus*).

The Middle Miocene German *Mops monslapidensis* (Rachl, 1983; formerly *Meganycteris monslapidensis* before synonymy with *Mops* by Legendre, 1985) differs from the Riversleigh species in: lack of the P_4 metaconid; lack of paraloph and metaloph on M^1 ; presence of

crests on M^1 linking the hypocone to the postprotocrista; reduced M^3 ; having P_2 and P_4 obliquely oriented in the lower tooth row; and lack of antero-posterior compression of the lower molar trigonids.

Other Tertiary molossids listed in Table 2 (*Tadaridinae* indet.; ?*Nyctinomus* sp.; *Vespertilionoidea*, ?*Molossidae*; and ?*Chiroptera*

cf. Molossidae) are at present too poorly-known to allow useful comparisons with the Riversleigh fossil species.

DISCUSSION

Petramops creaseri is referred here to Legendre's (1984b, p. 426) molossid subfamily Tadaridinae on the basis of its well-developed heel on M¹ and its nyctalodont lower molars. Features that exclude it from the subfamilies Molossinae and Cheiromelinae (Legendre, 1984b, p. 425) are its tall isolated hypocone, its slightly reduced P₂ and its lower molars with well-developed paraconids.

The phylogenetic position of *Petramops* within the Tadaridinae is more difficult to determine. There is still much debate about the interrelationships of extant higher-level molossid taxa (e.g. Freeman, 1981; Legendre, 1984b) and the Tertiary history of this group is not well understood. However, on the basis of dental characters, an hypothesis of the phylogenetic relationships of *Petramops* to all other adequately-described fossil and living molossids is given in Figure 7. Characters used in this analysis were selected on the basis of their preservation in the Riversleigh material as well as their apparent value in delimiting molossid species groups (see Freeman, 1981; Legendre, 1984a, b, 1985). Polarity of character states was determined by outgroup comparison in which the family Vespertilionidae was considered to be the sister group of the Molossidae (following, for example, Miller, 1907; see also Hand, 1984).

In this hypothesis, five higher-level taxonomic groups are recognised: species of *Mormopterus* s.l., *Nyctinomus* s.l., *Rhizomops*, *Petramops* and *Cuvierimops*. Species of *Cuvierimops* appear to be plesiomorphic with respect to all other molossids, and *Rhizomops* plesiomorphic to all living molossids. On the basis of these features, species of *Nyctinomops*, *Nyctinomus*, *Otomops*, *Chaerephon* and *Mops* form a monophyletic group, as do species of *Mormopterus* s.l. The Australian Miocene taxon *Petramops creaseri* appears to be most similar to species of *Cuvierimops* and *Rhizomops*, perhaps on the basis of symplesiomorphies, and to lie outside the radiation of living Australian molossids (see below).

The hypothesis is not wholly inconsistent with alternative hypotheses of tadaridine evolutionary relationships generated by other authors (see, for example, Freeman, 1981; Legendre, 1984b, 1985).

The most significant differences concern relationships of species of *Rhizomops*, *Otomops* and *Nyctinomops*. For example, in her review of extant species of the family Molossidae, Freeman (1981) recognized two main groups, the *Mormopterus*-like bats and the *Nyctinomus*-like bats, and considered *Nyctinomus* (*Nyctinomus*) (including *Rhizomops*) and *Mormopterus* s.l. to be the two most primitive groups to which all other genera can be related. In her monophyletic *Nyctinomus*-group she also included species of *Nyctinomops*, *Chaerephon*, *Mops* and *Otomops* (as well as *Eumops*, *Promops* and *Molossus*) and suggested close phylogenetic relationships between species of *Nyctinomus* and *Chaerephon*, *Chaerephon* and *Mops*, *Nyctinomus* and *Otomops* and between *Nyctinomus* and *Nyctinomops*. Freeman (1981) also placed '*Nyctinomus*' *brasiliensis* and *Nyctinomus aegyptiacus* phenetically close to species of *Mormopterus* and suggested a close phylogenetic relationship between species of *Nyctinomus* (*Nyctinomus*) and *Mormopterus* s.l. Species of *Mormopterus* (s.s. but including *Micronomus*), *Platymops* and *Sauromys* were recognized as a monophyletic group. Characters used in Freeman's cladistic analysis were ear shape, development of basisphenoid pits, degree of palatal emargination, wrinkling of the lips, wing shape, incisor number, reduction of P² and M³, and development of M¹ metaconule (?hypocone).

Legendre's (1984b, 1985) systematic review of extant and extinct tadaridines also recognised monophyly of *Mormopterus* s.l. as well as a group containing species of *Rhizomops*, *Nyctinomus*, *Chaerephon* and *Mops*. Species of *Otomops* were suggested to lie just outside this latter group while those of *Nyctinomops* may share a close phylogenetic relationship with species of *Rhizomops*. Legendre (1985) suggested that species of *Rhizomops* may be descendants of the *Cuvierimops* lineage, a lineage which may also have spawned the *Nyctinomus* s.l. species group. Molossid stock of similar grade was thought (Legendre, 1985) to have given rise to species of *Mormopterus* s.l.

Irrespective of the true phylogenetic position of species of *Rhizomops*, *Otomops* and *Nyctinomops*, dental features used in this study place the Riversleigh fossil molossid outside the radiation of living Australian molossids. The Miocene fossil appears to lack several derived traits exhibited by living Australian molossids that exclude it from the *Mormopterus* s.l. and *Nyctinomus* s.l. species groups. These derived

features lacking in *Petramops creaseri* include: myotodonty of lower molars; P₄ metaconid loss; loss of paraloph and metaloph on M¹⁻²; connection of M¹ hypocone to postprotocrista; transverse orientation of premolars in lower tooth row; and reduction of M³.

Although the precise relationship of *Petramops creaseri* to species of *Rhizomops*, *Cuvierimops*, *Mormopterus* s.l. and *Nyctinomus* s.l. is not yet clear, these lineages appear to have diverged sometime between the Late Eocene and Late Oligocene (Table 2). Species of *Cuvierimops* appear in the western European fossil record during the Late Eocene and disappear in the early Oligocene. Species of *Rhizomops* are known from the latest Oligocene and Middle Miocene of western Europe as well as the Pleistocene and Recent of central America. They are thought to have diverged from ancient Old World molossid stock (possibly the *Cuvierimops* lineage) before making an Early Oligocene trans-Atlantic crossing into South America (Legendre, 1984b; fig. 18b). Species of *Mormopterus* s.l. first appear in the Late Oligocene of South America and those of *Nyctinomus* s.l. in the Middle Miocene of Europe. *Petramops creaseri* is Australia's only known Tertiary molossid, occurring in the oldest Australian fossil deposits that have produced identifiable fossil bats.

As indicated by the superbly-preserved postcranial remains of the French *Cuvierimops parisiensis*, molossids had already developed their present-day wing structure, and possibly their capacity for long, sustained flight, by the Late Eocene. Living molossids, as represented by *Rhizomops brasiliensis*, exhibit an extreme adaptation in the morphology and biochemistry of their flight muscles for high energy expenditure over extended time periods relative to all other bats (Foehring & Hermanson, 1984). Today, *Rhizomops brasiliensis* migrates seasonally over 1,300 km across the American continent to reach the warmer latitudes of Mexico for the winter months (Fenton, 1983). During the Early Oligocene, an ancestral *Rhizomops* species appears to have made a trans-Atlantic crossing between Africa and South America (Legendre, 1984a, b, c). At that time the distance between these two continents may have been as much as 3,500 km (Webb, 1978) although offshore volcanic island arcs may have served to reduce that distance considerably (McKenna, 1980).

It seems likely that members of the *Petramops* lineage, like other molossids, were proficient long-distance fliers and that while water gaps separating Australia and Eurasia in, say, the Late

Eocene may have prevented molossids from reaching Australian shores, gaps existing by the Middle to Late Oligocene probably would not (Audley-Charles, 1981, fig. 4.5). Certainly, by the Early to Middle Miocene representatives of Old World bat families not recognised for sustained flight capability were well-established in Australia, the Riversleigh deposits being rich in hipposiderid and megadermatid fossil remains. In the case of at least the megadermatids, a number of independent colonization events appears to have occurred before the Early to Middle Miocene (Hand, 1985; Archer *et al.*, 1989), while the diversity of the Riversleigh hipposiderid fauna also strongly suggests that bats first entered Australia before the Early Miocene and that migration routes had been available even for bats not noted for long distance flight.

Because *Petramops creaseri* does not appear to have given rise to the groups of molossids now living in Australia, more than one colonization of Australia by molossids is envisaged. Subsequent or coincident molossid colonizations would have involved species of *Nyctinomus*, *Chaerephon* and *Mormopterus* (Freeman, 1981; Legendre, 1984b, c).

The family Molossidae is not well-represented in the Riversleigh fossil deposits, where it is currently known from what appears to be one individual recovered from the Gotham City Site. It is possible, however, that this may under-represent the family's status in Australia at that time. The Gotham City deposit is interpreted to comprise the remains of prey collected by the megadermatid *Macroderma* sp. Prey species apparently collected by this carnivorous megadermatid include small Miocene dasyurids, perameloids and acrobatids, juvenile petaurids, phascolarctids and pseudocheirids (these Gotham marsupials ranging from one-quarter to one-half the size of their modern counterparts), at least four hipposiderids and *Petramops creaseri*. Many mammal species preserved in the Gotham City deposit are typical of those found in contemporaneous Riversleigh deposits, but others, including *Petramops creaseri*, are unique to the Gotham City Site and appear to have been brought from outside the immediate environment by megadermatids.

The immediate palaeoenvironment of the Middle Miocene Riversleigh deposits is considered to have been dense rainforest (Archer *et al.*, 1989). Molossids (with their high aspect wings) are less capable of manoeuvring in confined spaces than, for example, hipposiderids (Hill & Smith, 1984) and, by modern analogy, would be expected to

have been foraging primarily in open areas above or at the edges of the canopy rather than within the lower, more cluttered levels of the rainforest. The very large Gotham megadermatid may have been capable of feeding in both areas, ambushing vertebrate prey within the forest and at its edges as its descendant *Macroderma gigas* appears to do today (Van Dyck, 1980; Tidemann *et al.*, 1985). Nevertheless, a fast, high-flying and possibly crevice-dwelling molossid presumably would not be easy prey for a megadermatid and may explain why molossids are poorly represented in the Gotham City deposit itself. Alternatively, the Gotham molossid and megadermatid may have been sharing the same diurnal roost, although Tertiary molossids do not appear to have been as cavernicolous as their contemporaries and are more commonly preserved as whole skeletons in strictly lacustrine deposits (Sige, 1971).

In summary, *Petramops creaseri* appears to be a primitive molossid that cannot be referred to species groups now living in Australia. Its affinities probably lie with ancient lineages represented in European Eocene and Oligocene deposits, lineages which may persist in the living American species *Rhizomops brasiliensis*. If the *Petramops* lineage is assumed to have been more capable of long distance flight than its Riversleigh hipposiderid and megadermatid contemporaries, then it is likely that it first colonized Australia well before the Early Miocene.

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LITERATURE CITED

- ADROVER, R. 1968. Los primeros Micromamíferos de la cuenca valenciana, en Bunol. (Nota preliminar.) *Acta Geológica Hispanica* 3: 78-80.
- AGUILAR, J.-P., BRANDY, L.D. AND THALER, L. 1985. La migration de Salobrena (Sud de l'Espagne). *Paléobiologie Continentale* 14: 3-17.
- ALLISON, F.R. 1978. The small molossid bats in Queensland. *Australian Mammal Society Bulletin* 5(1): 43.
1983. Little Northern Mastiff-bat, *Mormopterus loriae*. Eastern Little Mastiff-bat, *Mormopterus norfolkensis*. Beccari's Mastiff-bat, *Mormopterus beccarii*. p. 524, 525, 526 (respectively) In Strahan, R. (Ed.), 'The Australian Museum Complete Book of Australian Mammals'. (Angus and Robertson: Sydney).
- ANDERSEN, K. 1904. Chiropteran notes. *Ann. Mus. Civ. Stor. Nat. Genova* 3: 1-41.
- ARCHER, M., HAND, S.J. AND GODTHELP, H. 1986. 'Uncovering Australia's Dreamtime'. (Surrey Beatty and Sons: Sydney). 32pp.
- EVERY, R.G., GODTHELP, H., HAND, S.J. AND SCALLY, K.B. 1990. Yingabalanaridae, a new family of enigmatic mammals from Tertiary deposits of Riversleigh, northwestern Queensland. This volume.
- AUDLEY-CHARLES, M.G. 1981. Geological history of the region of Wallace's Line. p. 24-35. In Whitmore, T.C. (Ed.), 'Wallace's Line and Plate Tectonics'. (Clarendon Press: Oxford).
- BARROUR, R.W. AND DAVIS, W.H. 1969. 'Bats of America'. (University Press of Kentucky: Lexington).
- ENGELSSER, B. 1972. Die obermiozäne Säugetierfauna von Anwil (Baselland). *Naturforsch. Ges. Baselland, Tätigkeitsber.* 28: 37-363.
- FELTEN, H. 1964. Zur Taxonomie indo-australischer Fledermäuse der Gattung *Tadarida* (Mammalia: Chiroptera). *Senck. Biol.* 45: 1-13.
- FENTON, M.B. 1983. 'Just Bats'. (University of Toronto Press: Toronto).
- FLANNERY, T.F. AND ARCHER, M. 1987. *Trichosurus dicksoni* and *Strigocuscus gymnotoides*, two new fossil phalangerids (Marsupialia: Phalangeridae) from the Miocene of northwestern Queensland. p. 527-36 In Archer, M. (Ed.), 'Possums and Opossums: Studies in Evolution'. (Surrey Beatty and Sons and the Royal Zoological Society of New South Wales: Sydney).
- FOHRING, R.C. AND HERMANSON, J.W. 1984. Morphology and histochemistry of flight muscles in

- free-tailed bats, *Tadarida brasiliensis*. *Journal of Mammalogy* 63: 388-94.
- FREEMAN, P.D. 1981. A multivariate study of the family Molossidae (Mammalia, Chiroptera): morphology, ecology, evolution. *Fieldiana, Zoology* n.s. 7: 1-173.
- GEOFFROY, É. 1813. Description des Mammifères qui se trouvent en Égypte. p. 99-144 In Jomard, E.F. (Ed.), 'Description de l'Égypte ou recueil des observations et des recherches qui ont été faites en Égypte pendant l'Expédition de l'armée Française. Histoire Naturelle. Tome 2, Deuxième livre, (Volume IX), (L'Imprimerie Impériale: Paris).
- HAND, S.J. 1984. Bat beginnings and biogeography: a southern perspective. p. 853-904 In Archer, M. and Clayton, G. (Eds), 'Vertebrate Zoogeography and Evolution in Australasia'. (Hesperian Press: Perth).
1985. New Miocene megadermatids (Chiroptera: Megadermatidae) from Australia with comments on megadermatid phylogenetics. *Australian Mammalogy* 8: 5-43.
1987. Phylogenetic studies of Australian Tertiary bats: a summary of PhD thesis. *Macroderma* 3: 9-12.
- HILL, J.E. 1961. Indo-Australian bats of the genus *Tadarida*. *Mammalia* 25: 29-56.
1983. Bats (Mammalia: Chiroptera) from Indo-Australia. *Bulletin of the British Museum (Natural History)*, *Zoology* 45: 103-208.
- AND SMITH, J.D. 1984. 'Bats, a Natural History'. (Rigby: Adelaide).
- HONACKI, J.H., KINMON, K.E. AND KOEPL, J.W. (Eds). 1982. 'Mammal Species of the World'. (Allen Press and Association of Systematic Collections: Lawrence).
- KOOPMAN, K.F. 1984. Taxonomic and distributional notes on tropical Australian bats. *American Museum Novitates* 2778: 1-48.
- LAVOCAT, R. 1961. Le gisement de vertèbres miocène de Beni Mellal (Maroc). Étude systématique de la faune de mammifères. *Notes et Mémoires de la Service Géologique du Maroc* 155: 29-94.
- LEGENDRE, S. 1984a. Identification de deux sous-genres fossiles et compréhension phylogénique du genre *Mormopterus* (Molossidae, Chiroptera). *Compte rendu de l'Académie des Sciences, Paris* (2) 298(16): 715-20.
- 1984b. Étude odontologique des représentants actuels du groupe *Tadarida* (Chiroptera, Molossidae). Implications phylogéniques, systématiques et zoogéographiques. *Revue suisse de Zoologie* 91: 399-442.
- 1984c. Essai de biogéographie phylogénique des molossidés (Chiroptera). *Myotis* 21.22: 30-36.
1985. Molossidés (Mammalia, Chiroptera) cénozoïques de l'Ancien et du Nouveau Monde: statut systématique; intégration phylogénique des données. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 170: 205-27.
- AND SIGÉ, B. 1984. La place du "Vespertilion de Montmartre" dans l'histoire des chiroptères molossidés. *Actes Symp. G. Cuvier* (Oct. 1982): 347-61.
- MAHONEY, J.A. AND WALTON, D.W. 1988. Molossidae. pp. 146-50 In Walton, D.W. (Ed.), 'Zoological Catalogue of Australia'. Vol. 5. Mammalia. (Bureau of Flora and Fauna: Canberra).
- McKENNA, M.C. 1980. Early history and biogeography of South America's extinct land mammals. pp. 43-77 In Lockett, W.P. and Szalay, F.S. (Eds.), 'Evolutionary Biology of the New World Monkeys and Continental Drift'. (Plenum Publ. Corp.: New York).
- ROBINSON, P. AND TAYLOR, D.W. 1962. Notes on Eocene Mammalia and Mollusca from Tabernacle Butte, Wyoming. *American Museum Novitates* 2102: 1-33.
- MENU, H. AND SIGÉ, B. 1971. Nyctalodontie et myotodontie, importants caractères de grades évolutifs chez les chiroptères entomophages. *Compte rendu de l'Académie des Sciences, Paris* 272: 1735-38.
- MILLER, G.S.J. 1907. The families and genera of bats. *Bulletin of the United States National Museum* 57: 1-282.
- PAULA COUTO, C. de. 1956. Une chauvre-souris fossile des argiles feuilletées pléistocènes de Tremembé, état de São Paulo (Brésil). *Actes 4 Congr. Internat. Quat.* 343-47.
- AND MEZZALANA, S. 1971. Nova conceituação geocronológica de Tremembé, Estado de São Paulo, Brasil. *Acad. Brasil Cienc.*, An. 43: 473-88.
- RACHL, R. 1983. Die Chiroptera (Mammalia) aus den mittelmiozänen Kalken des Nordlinger Rieses (Süd Deutschland). Inaugural-Dissertation, Ludwig-Maximilians-Universität: München.
- REVILLIOD, P. 1920. Contribution à l'étude des chiroptères des terrains tertiaires. 2^e partie, *Mém. Soc. pal. suisse* 44: 63-129.
- SIGÉ, B. 1971. Anatomie du membre antérieur chez un chiroptère molossidé (*Tadarida* sp.) du Stampien de Céreste (Alpes-de-Haute-Provence). *Palaeovertebrata* 4: 1-38.
1982. Contributions à l'étude des micromammifères du gisement miocène supérieur de Montrédon (Hérault). 4. Les chiroptères. *Palaeovertebrata* 12: 133-40.
- HAND, S.J. AND ARCHER, M. 1982. An Australian Miocene *Brachipposideros* (Mammalia, Chiroptera) related to Miocene representatives from France. *Palaeovertebrata* 12: 149-71.
- TATE, G.H.H. 1952. Results of the Archbold Expeditions. No. 66. Mammals of Cape York Peninsula, with notes on the occurrence of rain forest in Queensland. *Bulletin of the American Museum of Natural History* 98: 563-616.
- TIDEMANN, C.R., PRIDDEL, D.M., NELSON, J.E. AND PETTIGREW, J.D. 1985. Foraging behaviour of the Australian Ghost Bat, *Macroderma gigas* (Microchiroptera: Megadermatidae). *Australian Journal of Zoology* 33: 705-13.
- TROUGHTON, E. le G. 1967. 'Furred animals of Australia'. 9th ed. (Angus and Robertson: Sydney).

- VAN DYCK, S. 1980. Ghost Bat and death cries from the rainforests of McIlwraith Range, Cape York Peninsula. *N. Qd Nat.* **45**: 3-5.
- VAUGHAN, T.A. 1966. Morphology and flight characteristics of molossid bats. *Journal of Mammalogy* **47**: 249-60.
- WEBB, S.D. 1978. A history of savanna vertebrates in the New World. Part II: South America and the great interchange. *Annual Review of Ecology and Systematics* **9**: 393-426.
- WILEY, E.O. 1981. 'Phylogenetics: the Theory and Practice of Phylogenetic Systematics'. (John Wiley and Sons: New York).
- WOODBURNE, M.O., TEDFORD, R.H., ARCHER, M., TURNBULL, W.D., PLANE, M.D. AND LUNDELIUS, E.L. 1985. Biochronology of the continental mammal record of Australia and New Guinea. *Special Publication, South Australian Department of Mines and Energy* **5**: 347-63.